THE BIOLOGY OF MOSSES

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PREFACE

The last two decades have seen a resurgence of interest in the lower plants and particularly in the lichens. Thus books have been published on the effects of air pollution on lichens, on their ecology and on their biology. In contrast, no book on the biology of mosses is currently in print. Much research has now been completed on the physiology and biology of these plants and this has provided the data base for the present book. Also included are accounts of the value of mosses for pollution monitoring and of the traditional uses of these plants by man. Lighter material has been interwoven with the more academic aspects of the subject to make the book more enjoyable and easier to assimilate for both students and naturalists.

The texts of mosses in English, available to students, are rather limited. The small volume by Dr E.V. Watson, *The Structure and Life of Bryophytes*, deals mainly with structural and morphological aspects while that by Dr N.S. Parihar, *Introduction to the Embryophyta, Vol. 1, Bryophyta*, provides excellent and detailed accounts of a selected number of bryophytes but has very limited information on the physiology, biology or economic importance of the group. Finally, the volume by Dr P. Puri, *Bryophytes: a Broad Perspective*, is now out of print. There is thus a need for an additional volume and it is hoped that the present book will not only fill the gap, but also stimulate further interest in the experimental and applied aspects of this remarkable group of plants.

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CHAPTER 1
STRUCTURE, HISTORY AND ILLUSTRATION

1 STRUCTURE AND CLASSIFICATION

Mosses are widely recognized even though the individual plants are small and not conspicuous. This is because mosses often form extensive green carpets which bear the characteristic brown capsules in late spring. Spores released from the capsules germinate to give green filaments termed protonemata. The green leafy moss shoots which will bear the capsules arise from the protonemata. There are some 15,000 species of mosses and the variation in the size and shape of both the leafy shoots and capsules is very great indeed. The largest of all mosses is *Dawsonia* from Australasia whose shoots commonly grow to more than 20 cm high but may reach 70 cm when found under ideal conditions in wet shady forests. The aquatic moss *Fontinalis*, common in the Northern Hemisphere, can grow to a similar size. At the other extreme are the earth mosses such as *Ephemerum* which may be less than half a millimetre high.

The stems of the large robust mosses such as *Dawsonia* or the cosmopolitan hairy cap moss, *Polytrichum*, are composed of several different types of tissue. Each is specialized for the conduction of water, food or for assisting with mechanical support. However, the stems of most mosses are not like this but are made up of undifferentiated cells with the exception of a small central strand and a narrow band of thickened cells in the outer region. Even these modifications are absent in many genera. Thus the mechanical and conducting tissues of moss stems do not compare in efficiency or complexity with those found in ferns, fern allies, coniferous plants or flowering plants. In addition, mosses lack true roots and only possess tufts of rhizoids which attach them to their substrates. The leaves of mosses are spirally arranged and usually lance-shaped with pointed tips. They often sheath the stem at the base, so providing spaces where water is held by capillary attraction. Moss leaves are normally one cell thick except in species where there is a thickened border or leaf vein. Often the margin is toothed and the cells from which the leaf is composed may be of distinctive

shape or sculpturing which aids in the identification of various species.

There are three major groups of mosses (Fig. 1.1). Firstly, there are the granite mosses (Andreaeaopsida), *c.* 100 species which form widely scattered blackish or dark red-brown patches on rocks in mountainous or arctic regions. The blackness, habitat and small size of the individual plants are characteristic of the group. The capsules are unique among mosses in that they open by a number of longitudinal slits. The second group are the peat mosses (Sphagnopsida) *c.* 350 species, which are abundant in acid mires (bogs) and are immediately recognizable by their distinct features. They form the bright green (or occasionally reddish) clumps on mires or on acid boggy ground. At the apex of the *Sphagnum* plant, the branches are usually tightly packed together to form a moplike head. Below these, there are divergent branches which spread widely from the stem and, slimmer, inconspicuous branches that run down parallel to the stem. All these are clothed in leaves composed of large dead cells surrounded by narrow green (or sometimes red-pigmented) living cells. The dead cells have pores and thickenings and readily become filled with water. Thus the water holding capacity of a *Sphagnum* plant is up to 20 times its dry weight and, this characteristic has been made use of by man in many ways (see Chapter 12). The lids of the capsules of peat mosses are thrown off and the spores violently dispersed all at one time. The third and largest group of mosses are the true mosses (Bryopsida) *c.* 14,000 species. The members of this group vary enormously in size and shape but there are two basic growth habits; tuft forming (acrocarpous) and carpet forming (pleurocarpous). In the former, buds formed on the extending green filaments, which develop from a germinating spore, grow upwards to form a compact tuft. The individual shoots are unbranched to sparingly branched with groups of rhizoids at the base. These sometimes run along the surface of the shoot assisting capillary conduction of water up the tuft. Such mosses are frequently epiphytes on rocks or on the crowns of trees. In contrast, the shoots of the carpet forming mosses branch frequently and tend to be horizontally orientated. A series of loosely overlapping plants make up the moss carpets which are a feature of many forest floors.

The capsules that develop on the leafy shoots of true mosses are borne on short stalks (setae) and are protected by a cap of tissue called the calyptra. This falls off to reveal the fully grown capsule which usually has a lid. This in turn is shed and normally exposes a series of

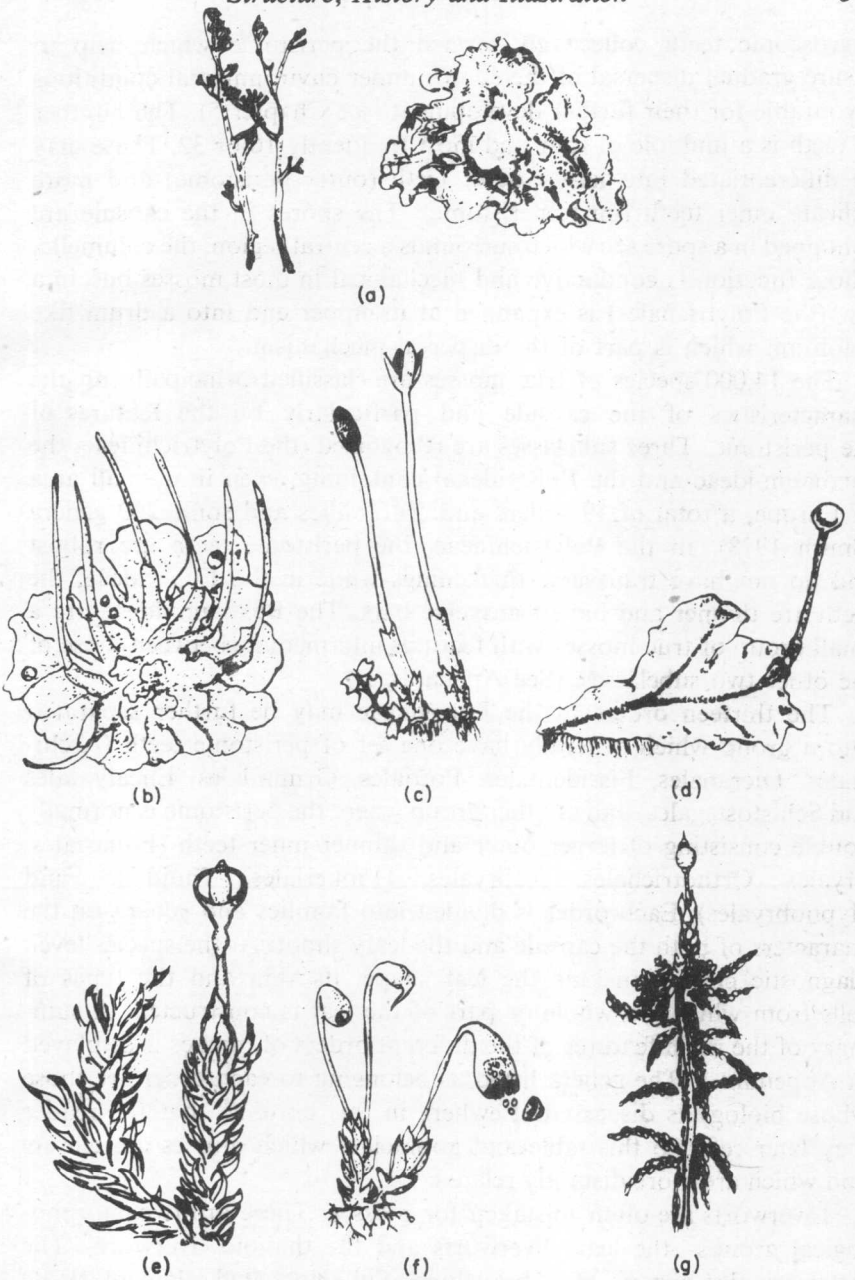

Fig. 1.1 Line drawings to illustrate the macroscopic differences between lichens (a), hornworts (b), leafy liverworts (c), thalloid liverworts (d), and mosses. The main groups of mosses are granite mosses (e), true mosses (f), peat mosses (g) (drawn by R. West).

hygroscopic teeth collectively termed the peristome which help to ensure gradual dispersal of the spores under environmental conditions favourable for their further development (see Chapter 5). The number of teeth is a multiple of four and most frequently 16 or 32. These may be differentiated into larger outer teeth (outer peristome) and more delicate inner teeth (inner peristome). The spores in the capsule are contained in a spore sac which surrounds a central region, the columella, whose function is conductive and mechanical in most mosses but, in a few (the Polytrichales) is expanded at its upper end into a drum like epiphram which is part of the dispersal mechanism.

The 14,000 species of true mosses are classified principally on the characteristics of the capsule and particularly on the features of the peristome. Three subclasses are recognized (the Polytrichideae, the Buxbaumiideae and the Eubryideae) containing, even in a small area of Europe, a total of 19 orders and 50 families and some 200 genera (Smith 1978). In the Polytrichideae, the peristome teeth are robust and do not have transverse thickenings while in the Eubryideae, the teeth are thinner and have transverse bars. The Buxbaumiideae are a small group of true mosses with features intermediate between those of the other two subclasses. (See Appendix 1.)

The thirteen orders in the Eubryideae may be further separated into a group which generally have one set of peristome teeth (Archidiales, Dicranales, Fissidentales, Pottiales, Grimmiales, Encalyptales and Schistostegales) and another group where the peristome is normally double consisting of larger outer and thinner inner teeth (Funariales, Bryales, Orthotrichales, Isobryales, Hookeriales, Thuidiales and Hypnobryales). Each order is divided into families and genera on the characters of both the capsule and the leafy shoot. At the species level, diagnostic criteria include the leaf shape, its vein and the types of cells from which the whole or part of the leaf is constructed. A summary of the main features of the different orders of mosses is displayed in Appendix 1. The genera listed as belonging to each order are those whose biology is discussed elsewhere in this book so that the reader may later refer to this table and appreciate which mosses are closely and which are more distantly related.

Liverworts are often mistaken for mosses. There are two morphological groups—the leafy liverworts and the thalloid liverworts. The latter usually consist of a branching, flat, elongated plate of tissue which grows closely adpressed to damp soil. The leafy liverworts bear much more resemblance to mosses but close examination reveals that

the leaves are seldom single-pointed (frequently they are two lobed, and have no midrib) and are normally in two or three rows rather than being spirally arranged on the stem as in mosses. In addition the capsules of liverworts release their spores by splitting into four valves and possess specially thickened cells, the elators, which facilitate spore dispersal. However, the life history of both liverworts and mosses is similar so that they are placed in the same phylum the Bryophyta along with another small rare group the hornworts. They look like thalloid liverworts but have long pointed capsules which have no stalk and split into two valves at the apex (Fig. 1.1). Lichens are another group of plants which are often confused with mosses and are often discussed with them. They are, however, quite distinct in being a symbiotic association between a fungus and an alga that forms a composite plant which does not have leaves. In addition lichens are usually greyish rather than being bright green and they produce fungal fruit bodies not capsules (Richardson 1975).

2 HISTORY OF THE STUDY OF MOSSES

The Greek, Theophrastus, who lived *c.* 300 B.C. does not mention mosses (Hort 1916). Nor are they shown in the illustrations of the writings of Dioscorides who was a physician to the Roman legions and died about 77 A.D. (Dioscorides 1763–1773). He travelled widely with the legions during the time of Vespasian and Nero and described and illustrated the plants known in his day. Mosses also do not seem to have been important in medicine in Saxon times (Cockaine 1864) nor are they illustrated in the earliest herbals (e.g. Anon. 1484). Lichens on the other hand, which were of more value in medicine, were illustrated in such renaissance books. Later, mosses as well as lichens were illustrated in herbals. They were listed under Musci which is Latin for mosses but the group Musci was not well defined in these herbals. For example, in the Niewe Herball (1576) there are several illustrated descriptions that are now known to be one moss (*Polytrichum*), two lichens, one fern ally, one flowering plant and two seaweeds (Dodoens 1576). The illustration of the moss, then called the golden maidenhair moss, is shown in Fig. 1.2 but, according to the herbal 'men use not this moss in medicine'.

The development of botany as a science distinct from pharmacognacy (the study of plants to discover drugs of use in the treatment

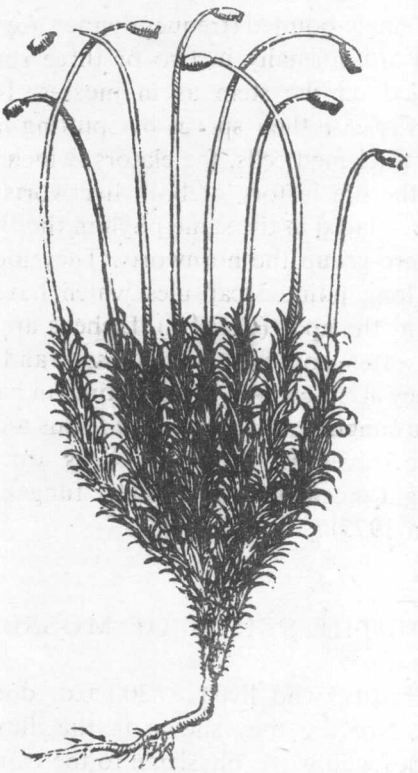

Fig. 1.2 The earliest illustration that could be found of a moss with both leafy shoots and capsules. The moss was then called the golden maidenhair moss and is now known as the hairy cap moss, *Polytrichum* (Dodoens 1576).

of disease) led to extensive collections and detailed descriptions of plants without reference to their medicinal value. Professor Johann Dillen was induced to come to Oxford from Germany and in the tradition of the times latinized his name to Dillenius. He wrote a book entirely devoted to mosses and their allies (Dillen 1741) entitled *Historia Muscorum*. This contains the descriptions of the lichens, club mosses and quillworts (fern allies), liverworts and mosses which were known in his time. Twenty-seven plates were used to illustrate the mosses and familiar genera such as *Bryum*, *Fontinalis*, *Hypnum*, *Mnium*, *Polytrichum* and *Sphagnum* are to be found. A clear improvement, over the early herbals, is evident in the quality of illustration and in the number of features observed (Fig. 1.3). The function of the observed structures intrigued the early botanists and was the subject of lively

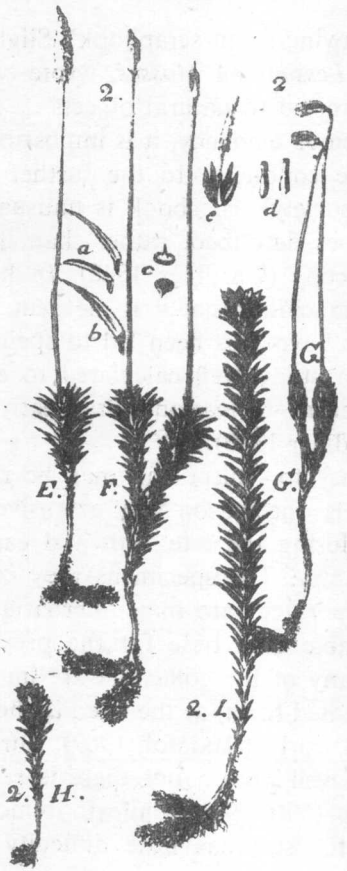

Fig. 1.3 A later illustration of *Polytrichum*, 1741. Note the greater detail of the moss shoots and the capsules with opercula and calyptrae (Dillen 1741).

debate and investigation. They attempted to discover the complete life history of mosses but this proved a difficult task (see next section): indeed algae, liverworts, mosses and ferns became known as the cryptogams which literally means 'the hidden sex' plants.

Towards the middle of the last century, moss study had changed direction once again as the pursuit of natural history and plant collecting by amateurs came into vogue. Thus Stark (1860) in his *Popular History of British Mosses* says that '*Ptilium crista-castrensis* is one of the prizes that botanical tourists should endeavour to carry south (from Scotland), as a remembrance of the land of brown heath and shaggy wood, for its feathery branches suit admirably either for the scientific

cabinet or the drawing-room scrapbook'. Slightly earlier, Gardiner in his book *Twenty Lessons on Mosses*, wrote 'were the youthful mind more generally directed to natural objects . . . rather than to matters of frivolous or vicious tendency, it is impossible to say to what extent this might not be conducive to the further advancement and well being of human society'. His book is unusual in that pressed specimens of the mosses described, rather than illustrations, were incorporated in each copy (Gardiner 1848). In his second book on the same subject he concludes that it is pleasant to reflect that 'many of my young readers have thus been led to spend some portion of their leisure hours in a study well calculated to afford them not only a healthy and innocent recreation but greatly to refine and elevate their minds' (Gardiner 1849).

Mosses are easy to collect and may be readily preserved simply by drying which is one reason why extensive collections were made by taxonomists during the late 19th and early 20th centuries from almost every country. The specimens they collected were described, named and incorporated into major herbaria around the world providing an invaluable data base for the preparation of moss floras. The names of many of the collectors are immortalized and familiar, though in abbreviated form, as the cited authority for the moss names used in published works (Rudolph 1969). Europe and North America are bryologically well known but there is still much to be done by taxonomists there (Vitt 1981) while in remote places such as New Guinea, a collector still has little difficulty in finding undescribed species.

During the first half of the present century, studies on the physiology and genetics of flowering plants attracted most attention and mosses were rather neglected. However, in the last two decades many techniques have been adapted for investigations on mosses (Sarafis 1971). Thus great advances have been made in understanding the physiology, genetics and biology of mosses so that bryology is once again regarded as an exciting and popular field of study within botany.

3 DISCOVERY OF THE LIFE HISTORY OF MOSSES

Although the herbals of the renaissance period illustrated a number of mosses, in some cases with capsules (see Fig. 1.2) the life history